Identifying drivers of forest resilience in long-term records from the Neotropics

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Abstract

Here we use 30 long-term, high-resolution palaeoecological records from Mexico, Central and South America to address two hypotheses regarding possible drivers of resilience in tropical forests as measured in terms of recovery rates from previous disturbances. First, we hypothesise that faster recovery rates are associated with regions of higher biodiversity, as suggested by the insurance hypothesis. And second, that resilience is due to intrinsic abiotic factors that are location specific, thus regions presently displaying resilience in terms of persistence to current climatic disturbances should also show higher recovery rates in the past. To test these hypotheses, we applied a threshold approach to identify past disturbances to forests within each sequence. We then compared the recovery rates to these events with pollen richness before the event. We also compared recovery rates of each site with a measure of present resilience in the region as demonstrated by measuring global vegetation persistence to climatic perturbations using satellite imagery. Preliminary results indeed show a positive relationship between pre-disturbance taxonomic richness and faster recovery rates. However, there is less evidence to support the concept that resilience is intrinsic to a region; patterns of resilience apparent in ecosystems presently are not necessarily conservative through time.

Keywords

Resilience, Palaeoecology, Forest, Neotropics, Disturbance, Pollen

Background

In the present context of global change, where ecosystems are likely to be exposed to an increase in disturbances [1], a knowledge of the factors that make ecosystems resilient has become increasingly important. Such knowledge is critical for determining landscapes that may be better able to withstand climate change and other environmental disturbances, especially in forested systems, which provide many important ecosystem services [2]. There are two forms of resilience to consider: the first known as ecological resilience [3,4], measured by recovery rates from a disturbance event and calculated in this manuscript, and the second being engineering resilience or persistence [5], referring to how long an ecosystem can withstand a disturbance before changing to an alternative state.

To date, several palaeoecological studies have addressed ecological resilience [6–9], but these have tended to only look at one individual system, and few have attempted regional syntheses to address specific hypotheses regarding the nature and underlying drivers of resilience [6]. In this study, we examined records from 30 high-resolution palaeoecological datasets across Neotropical forest ecosystems. The sites showed evidence of one or more past forest disturbance events, such as fire, hurricanes or anthropogenic impacts, as well as displaying spatial variation in recovery rates to these events. Using these records we address two hypotheses related to resilience [3]. First, the insurance hypothesis [10], which states that more diverse ecosystems have greater resilience. Second, the hypothesis that resilience is due to a combination of location-specific abiotic factors [11], and thus some locations demonstrate a constancy of resilience through time due to these abiotic features.

Methods

Identifying disturbance events

We selected high resolution, well-dated palaeoecological datasets from the Neotropics (Figure 1, Table 1) covering the time period from the Late Glacial to the present (i.e. from 13,000 calibrated years before present (cal yr BP)) and spanning a large gradient in vegetation persistence as measured by the Vegetation Sensitivity Index (VSI, [12]. The different forest types under analysis include pine, tropical dry-deciduous, tropical semi-deciduous, Andean, Subpáramo, montane, gallery, cloud and rain forests (Table 1). To objectively identify disturbance events for each sequence, we applied a threshold method based on the percentage of the sum of pollen from forest taxa per Pollen Assemblage Zone (PAZ). To achieve this, first the counts of pollen grains per sample belonging to all terrestrial taxa were square-root transformed [13] and hierarchically clustered through time to determine statistically significant PAZs [14] of the pollen sequences. These analyses were done by using the Rioja package [15] in the R software [16]. For each sequence, percentages of the pollen taxa from the main forest type present within the sequence were summed together. Within each PAZ, mean and standard deviation for the sum of percentages of the forest taxa were calculated. Disturbance events within the sequences were defined as: 1) having a forest percentage sum of less than the mean minus one standard deviation per PAZ (i.e. $<\mu-1\sigma$, where μ is the mean and σ is the standard deviation), making this our threshold value to identify disturbances, 2) displaying more than one sample within a disturbance event, 3) recording a clear start

and end of the disturbance event within the sequence and 4) having a mean temporal resolution below 100 years (see details in the Electronic Supplementary Material (ESM) 1 and 2). The second criterion was added to reduce the probability of counting stochastic variations in pollen percentage sums as a disturbance event, while clear starting and ending points in criterion three refer to local maxima in the arboreal sum before and after disturbance [6].

In a previous study from the tropics that used recovery rates following disturbance in fossil pollen records to measure resilience [6], the recovery rates were defined as a percentage increase of arboreal pollen abundance per year relative to the pre-disturbance level. We applied this previously published equation [6] (eq. (1), ESM 2),

$$RR = \frac{\left(\frac{Fmax - Fmin}{Fpre - Fmin} * 100 \right)}{Trec} \quad (1)$$

which uses the following identifiable points within the sequences: the lowest forest percentage sum within a disturbance (Fmin), the highest forest percentage sum after recovery (Fmax), the percentage sum prior to the disturbance start (Fpre) and the time of recovery (Trec, ie. from Fmin to Fmax) in calibrated years before present (cal yr BP). We calculated recovery rates per disturbance and mean recovery rates per study site. In addition, in order to assess whether forests recovered to a similar community assemblage as their pre-disturbance state or to a different assemblage, we calculated squared chord distance coefficients [17] between pre- and post-disturbance samples following the approach of Bennion et al. 2004 [18]. Samples with a coefficient of 0 indicate communities that are identical to each other, while those with a coefficient of 2 are completely different. As in [18], we chose the 5th percentile cut-off value of 0.48, below which there is insignificant assemblage change between samples. For more details about dataset selection, chronology, statistics, overall methodology and raw data, please refer to the ESM 3, ESM 4 and [19].

Extracting pollen richness and vegetation sensitivity index for each location and disturbance event

To test the insurance hypothesis, i.e. that more diverse ecosystems have greater resilience, pollen richness, a proxy for vegetation richness [20–23] before each disturbance event was estimated using the counts of pollen belonging to terrestrial taxa and this was compared to recovery rates. We hypothesised that those sites with higher pre-disturbance pollen richness would have faster recovery rates. To reduce the sampling bias that affect richness estimations, which occurs when analysts count different amounts of pollen grains per sample, we performed rarefaction analysis [24] on all sequences by using a minimum pollen sum of 100 grains. We used a generalised linear model with variance weighting by study site to test the relationship between pollen richness and $\log_{10}(x+1)$-transformed recovery rates. The log transformation was chosen to reduce the effect of outliers [25]. The following variables: richness, latitude, altitude and sample resolution, were included in the initial model and tested for significance and influence on model performance following the Akaike information criterion [26].

To test the abiotic hypothesis i.e. that resilience is due to a combination of location-specific abiotic factors, we used a linear regression model to test the relationship between spatial patterns in present-day vegetation persistence, as measured by the Vegetation Sensitivity Index (VSI, [12]) to recovery rates from the past at the same locations. The VSI quantifies vegetation sensitivity over 14 years (2000-2013) in terms of productivity to solely abiotic factors (i.e. climatic factors such as water availability, air temperature and cloudiness) on a 5km resolution at the global scale, whereby a high sensitivity value indicates low persistence and vice versa. To link this measure up with longer-term vegetation dynamics as obtained from the fossil pollen sequences extracted from the lake sediments [27], we extracted the VSI value from the point location of the fossil study site from the shapefile version of the VSI by using ArcGIS (v. 10.6), software. We hypothesised that those sites with faster recovery rates in the past also show greater persistence to climatic perturbations from 2000 to 2013. All model calculations were done in the nlme package available in R software [16,28].

Results

We analysed 30 sedimentary records from the Neotropics (Figure 1) and a total of 59 disturbance events. Three sequences were excluded from further analyses for not meeting the disturbance identification criteria (ESM 1). During the extracted disturbance events, all of these records were sampled at a high temporal resolution, with a mean sample resolution across sequences of one sample every ca. 40 years (37.7±27.5 years, ESM 1). This high temporal sample resolution is crucial to ensure that the generational change of trees in these forested environments is captured and to reduce the possibility of missing consequent disturbance events. For example, previous studies have identified that it takes between 30 to over a 1000 years for tropical forests to recover following disturbance [6].

The range of recovery rates (in percentage of forest pollen abundance increase per year relative to the levels prior to disturbance) varied from 0.1 to 24.6 (or 0.04 to 1.41 after $\log_{10}(x+1)$ transformation, ESM 5), while pre-disturbance palynological richness values (RichnessPre) ranged between 3.7 to 25.3 different pollen taxa per sample, being highest close to the Equator. The range of VSI included in our study went from 8.1, indicating highest persistence to climatic factors to 55.7, displaying lowest persistence to climatic perturbations (ESM 1, Table 1).

Taking all disturbances together, the variables RichnessPre and the mean temporal resolution of samples within a disturbance (TResolDist) were significant in explaining recovery rates (p-value <0.001, Figure 2A, Table 2a, ESM 6). This indicates that a high sampling resolution may enable a more accurate detection of forest recovery, while a potential earlier recovery might be missed in records that have a longer time interval between samples. Despite this effect of sampling resolution on the calculated recovery rates, RichnessPre still has a significant positive effect on the calculated recovery rates.

Regarding our second hypothesis, there is a slightly negative relationship between mean recovery rates per study site ($\log_{10}(x+1)$-transformed) and vegetation sensitivity index at the corresponding sites (Figure 2B), which would be in agreement with our second hypothesis. However, this VSI was not a significant variable within the linear regression model (Table 2b). Our dissimilarity analyses showed that only six of 59 assemblages showed significant change pre- and post-disturbance (Figure 2C, ESM 1 Table 1). This indicates that forests seem to recover to a similar composition as found before the disturbance.

Discussion

Our study indicates that within our analysed temporal scale of several thousands of years, resilience properties of a system are generally not location specific and seem not to be associated with the unique set of abiotic factors present. Rather, other factors related to the vegetation assemblage itself, such as biodiversity, appear to be more important.

Previous research has already found a positive effect of biodiversity on the resilience of plant communities, however, most of this research has focused on ecosystems with short generation times (i.e. grasslands, agricultural systems) and on recent timescales [29,30]. To our knowledge this is the first time this relationship has been demonstrated across the Neotropics through time.

Even though the records chosen in this study have not been sampled continuously, the mean resolution of samples within disturbances (ca. 40 years) roughly corresponds to rates of disturbance i.e. from fire in highly fire prone ecosystems (e.g. fire return intervals of 30 years in Mediterranean ecosystems [31]). In our study of tropical forests, the insurance hypothesis [10], stating that more complex systems recover faster from disturbance, is supported by our results, showing the importance of biodiversity to enable forests to recover from disturbances. Our findings are also in agreement with dynamic simulation modelling results of temperate forest ecosystems, which have previously demonstrated that tree diversity positively influences stable forest productivity over time [32]. Possible explanations as to why biodiversity increases ecosystem's resilience include the positive effect of different responses of species to fluctuations, also taking into account different response speeds [32,33] and the fact that there will be a number of species with similar functions thus able to replace the functions of the species lost [10]. Using long-term data from palaeoecological records, as has been done in this study, could provide important further avenues of research into these relationships by looking, for example, at individual taxon traits in those records that demonstrate faster recovery rates.

The lack of a strong relationship between current vegetation persistence patterns at sites and faster recovery rates in the past, may possibly be explained by shifting ecotone boundaries and baselines. Thus, under different climatic conditions in the past, these boundaries have shifted, as can be seen in changing treeline altitudes through time [34], displacing the physical location at which an ecosystem is more sensitive to change. However, we also need to consider the differences in the temporal scale that affect our analyses. We have compared a VSI based on 14 years of data, which in most cases, will not record a single generation of trees, to recovery rates issuing from forest dynamics covering thousands of years and representing multiple generations. Additionally, differences in the pollen source area from large to small lakes and the pixel size of 5km^2 of the VSI data will not always be comparable and smaller scale abiotic features such as soil type or slope and aspect cannot be reflected on such large pixels. Nevertheless, a result emerging from our study is that the persistence apparent in these ecosystems presently, is not necessarily conservative through time. Thus abiotic factors, cannot alone be used to explain patterns of resilience; rather our results indicate that pre-disturbance taxonomic diversity is a better indicator of resilience of the system (as measured by recovery rates). This result suggests that conservation management efforts which aim to create resilient ecosystems by maintaining and enhancing biodiversity, are a good approach.

Conclusions

We have identified biodiversity of forests to be important for their resilience, highlighting the

necessity of promoting diverse ecosystems to ensure their provision of ecosystem services in a changing environment. Additionally, further research into which vegetation traits are associated with resilient ecosystems would be an important step towards managing resilient ecosystems for the future, as well as further insights into ecosystem stability.

Acknowledgements

We are grateful to all authors that have made their data available on Neotoma, to Peter Long for his help with the VSI index shapefile, to Dirk Enters for his advice regarding the record of Lago Alexio and to Daniele Colombaroli for sharing parts of his R-code [23] for diversity calculations.

Author contributions

KJW and CA conceived the study and lead the writing process; CA performed numerical analyses and wrote the R code with assistance and input from CT and NK. HB, JCB, GD, BFR, ZGC, GAI, HH, HN, MOV, BW and MJW provided their datasets along with interpretation advice. All authors made important contributions to the final manuscript. All authors agree to be held accountable for the manuscript's content and have approved its final version.

Data accessibility

All R scripts and parts of datasets (details on accessing Neotoma datasets are in the ESM) used for analyses are available under: https://doi.org/10.5061/dryad.xwdbrv19c. Description of the datasets can be found in the ESM 7.

Funding

This work was supported by the Swiss National Science Foundation (Grant number: P2BEP2_178414 to CA).

Conflict of interest statement

The authors declare no conflict of interest.

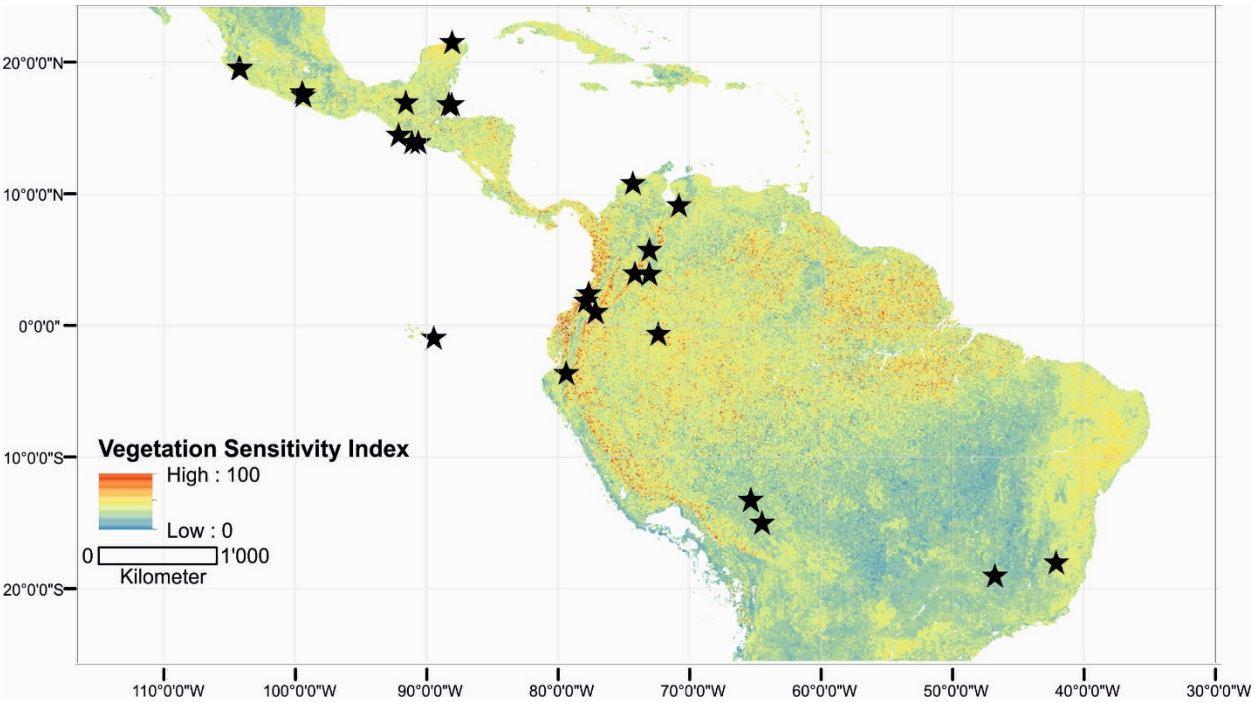

Figure 1: Distribution of study sites (black stars) in Mexico, Central and South America. Sites are displayed on top of a map with the current vegetation sensitivity index (VSI) as identified by Seddon et al. [12].

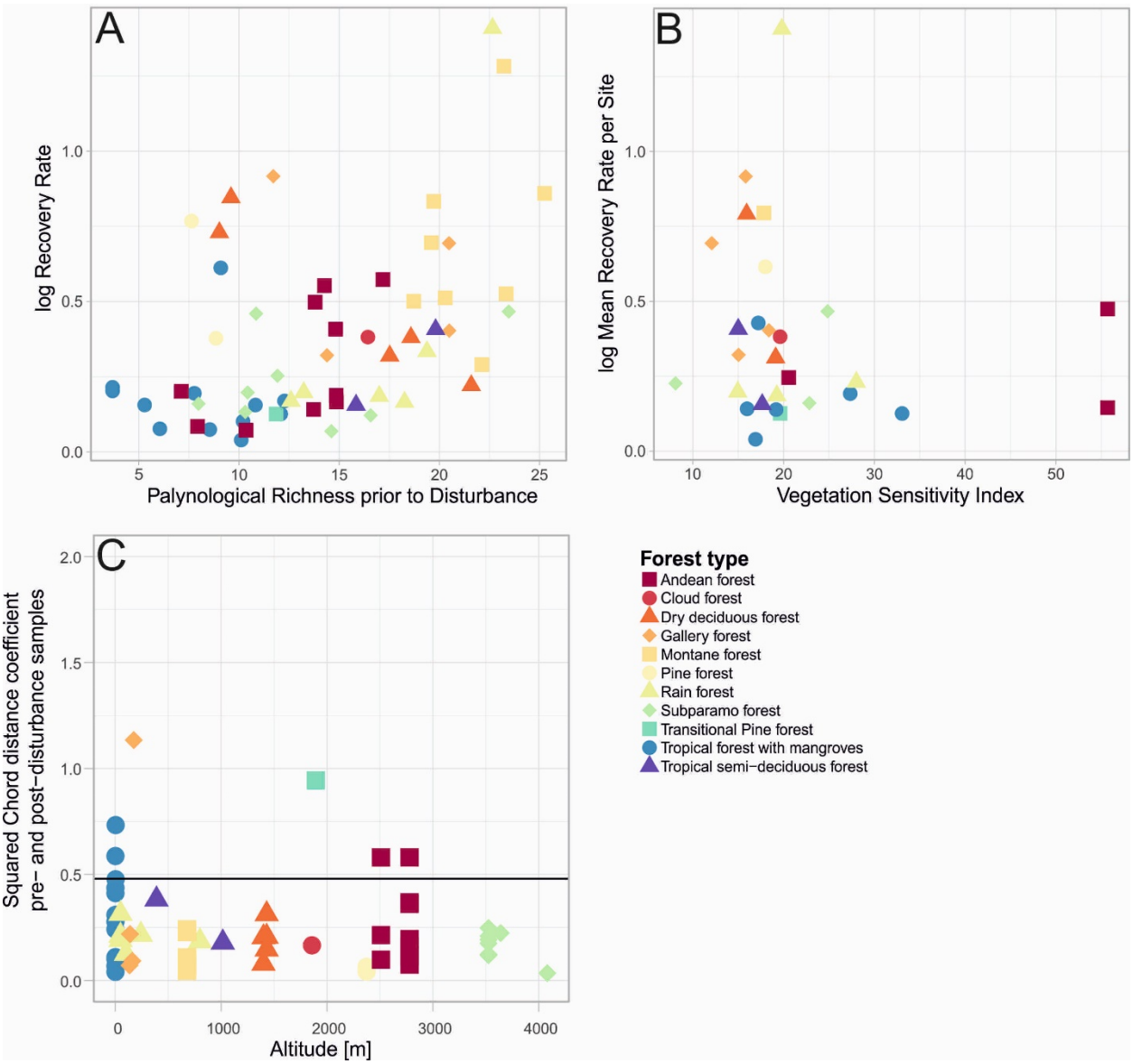

Figure 2: The relationships describing the two hypotheses to be tested. A) Palynological richness [number of different pollen taxa per sample] as a proxy for vegetation diversity vs recovery rates [percentage of forest pollen abundance increase per year, relative to pre-disturbance levels, $\log_{10}(x+1)$-transformed]. B) Vegetation sensitivity index (VSI) vs mean recovery rate ($\log_{10}(x+1)$-transformed) per each study site. C) Squared chord distance coefficient measuring similarity between pre- and post-disturbance samples along an altitudinal gradient. The horizontal black line represents the 5th percentile cut-off value of 0.48, below which there is insignificant assemblage change between samples.

Table 1: Study site details in latitudinal order from North to South						
Publication	**Site**	**Lon**	**Lat**	**Altitude [m asl]**	**Forest type**	**Number of disturbances per site**
Aragon-Moreno et al. 2012 [35]	Ria Lagartos	-88.07	21.58	2	Tropical forest with mangroves	2
Figueroa-Rangel et al. 2012 [36]	Transitional forest	-104.23	19.59	1894	Pine-Oak dominated forest	1
Figueroa-Rangel et al. 2010 [37]	Cloud Forest	-104.28	19.59	1858	Cloud forest	1
Figueroa-Rangel et al. 2008 [38]	Pine forest	-104.2	19.57	2374	Pine forest	2
Berrío et al. 2006 [39]	Lake Huitziltepec	-99.47	17.75	1430	Dry deciduous forest	3
Berrío et al. 2006 [39]	Lake Tixtla	-99.4	17.5	1400	Dry deciduous forest	2
Domínguez-Vázquez and Islebe 2008 [40]	Naja Lake	-91.59	16.99	800	Rain forest	1
Wooller et al. 2007 [41]	Twin Cays, TCC2	-88.1	16.83	0	Tropical forest with mangroves	3
Neff et al. 2006 [42]	TIL	-92.17	14.5	0	Tropical forest with mangroves	2
Larmon 2013 Master Thesis	Iztapa	-90.66	13.95	4	Tropical forest with mangroves	2
Neff et al. 2006 [42]	Sipacate - SIP99E	-91.15	13.93	0	Tropical forest with mangroves	2
Velez et al. 2014 [43]	Boca de Lopez	-74.33	10.85	0	Tropical forest with mangroves	1
Rull et al. 1987 [44]	Piedras Blancas	-70.83	9.17	4080	Subpáramo forest	1
Gomez et al. 2007 [45]	Pantano de Vargas	-73.07	5.78	2510	Andean forest	3
vdHammen and Hooghiemstra 1995 [46]	Laguna La Primavera	-74.16	3.98	3525	Subpáramo forest	6
Berrío et al. 2002 [47]	Laguna Mozambique	-73.05	3.96	175	Gallery forest	1
Velez et al. 2001 [48]	Laguna El Caimito	-77.69	2.45	50	Rain forest	3

Behling et al. 1998 [49]	Laguna Piusbi	-77.93	1.88	100	Rain forest	1
Epping 2009 Master Thesis	Laguna la Cocha	-77.15	1.08	2780	Andean forest	4
González-Carranza et al. 2012 [50]	Laguna La Cocha	-77.152	1.079	2780	Andean forest	3
Berrío et al. 2003 [51]	Quebrada del amor	-72.398	-0.60	242	Rain forest	1
Restrepo et al. 2012	El Junco	-89.48	-0.895	679	Montane forest	8
Adolf et al in prep. [52]	Laguna Vendada	-79.39	-3.61	3640	Subpáramo forest	1
Whitney et al. 2014 [53]	Laguna La Frontera	-65.35	-13.23	135	Gallery forest	1
Whitney et al. 2014 [53]	Laguna El Cerrito	-65.38	-13.25	140	Gallery forest	1
Whitney et al. 2013 [54]	Laguna San José	-64.5	-14.95	162	Gallery forest	1
Enters et al. 2010 [55]	Lago Alexio	-42.12	-17.99	390	Tropical semi-deciduous forest	1
Leyden et al. 1996 Thesis chapter	Lagoa Campestre de Salitre	-46.77	-19.0	1016	Tropical semi-deciduous forest	1

Table 2a: Results of generalised least squares model to test Hypothesis 1

Variables	Coefficient	Standard error	t-value	p-value
Intercept	0.3467423	1.261944e-05	27476.85	<0.001
RichnessPre	0.0067004	5.372250e-07	12472.26	<0.001
TResolDist	-0.0038703	8.149000e-08	-47493.63	<0.001

Model equation: $\log_{10}(RR+1) \sim$ RichnessPre + TResolDist, variance weighted by Site (i.e.weights = varIdent(form= ~ 1 | Site) as used in package "nlme" [28] in the R software); n = 59

RR: recovery rates, RichnesPre: Palynological richness per sample prior to disturbance, TResolDist: Mean temporal resolution of samples within a disturbance

Table 2b: Results of linear regression model to test Hypothesis 2

Variables	Coefficient	Standard error	t-value	p-value
Intercept	0.475075	0.132312	3.591	0.00135
VSI	-0.004270	0.005505	-0.776	0.44494

Model equation: $\log_{10}(mRR+1) \sim VSI$

mRR: mean recovery rates per site, VSI: vegetation sensitivity index

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